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Soil salinity as a selection pressure is a key determinant for the evolution of salt tolerance in Blue Panicgrass (*Panicum antidotale* Retz.)

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ABSTRACT

To assess the role of selection pressure in plant adaptation to saline environment, a hydroponic experiment was conducted on six *Panicum antidotale* Retz. populations collected from a wide range of habitats with varying selection pressure in the form of soil salinity. The soil electrical conductivity of six different habitats ranged from 3.39 to 19.23 dS m^{-1} and pH from 5.86 to 7.65. Plants of all populations collected from varying habitats were established in pots containing normal soil and allowed to grow for 6 months. Newly grown tillers from each plant were separated and 10 of them each formed a composite sample for a particular population. They were then transplanted in plastic containers each containing 10 l of half strength Hoagland's nutrient solution alone or with 150 mol m^{-3} NaCl. After 42 days growth in salt treatment, the populations collected form highly saline habitats proved to be more salt-tolerant compared with those from mild or non-saline habitats in terms of growth performance. The populations adapted to high salinity showed less decrease in leaf K^+/Na^+ and Ca^{2+}/Na^+ ratios under salinity stress. Moreover, under stress the salt-tolerant populations showed less reduction in photosynthetic capacity than the salt-sensitive populations. In addition, hyper-accumulation of organic solutes such as glycinebetaine and proline and thereby higher osmotic adjustment seemed to be associated with the higher degree of adaptability of the salt-tolerant populations to salt stress. From the data presented, it is plausible to conclude that selection pressure (soil salinity) must have been one of the important determinants bringing about the evolution of salt-tolerance trait in Blue Panic grass.

Introduction

Soil salinity is a major concern in the arid and semi-arid regions of the world. Various soil reclamation techniques have been devised to overcome this problem, but they are costly and hence are not practicable by poor farmers (Ashraf and Harris, 2005). Under this situation, exploration and cultivation of tolerant species offer a more practical solution for effective utilization of affected soils. Species found growing on natural saline habitats possess genetic variation, which is the basis of the evolution of salt-tolerant populations in response to the selection pressure of the habitats (Al Sherif, 2009; Ashraf et al., 2006; Nedjimi, 2009). However, the presence of appropriate genetic variation in the gene pool of a species and the occurrence of appropriate natural selection must interact determining the evolution of a particular character. The genetically based variation found in natural populations of plants often has not been explored, although the potential value of such genetic resources has recently been emphasized in modern research programs (Ashraf, 2004; Munns, 2002). In this situation, naturally adapted salt-tolerant plants provide an excellent material for investigating the adaptive mechanisms they use to encounter high concentrations of salt (Ashraf, 2003).

Panicum antidotale Retz., commonly known as Blue Panicgrass or Bluegrass, is distributed throughout the Indo-Pakistan region. It is found growing in a variety of soils and climatic conditions with a predominant distribution in arid and semi-arid regions (Cope, 1982). This tall grass is a coarse perennial that may attain a height of 2 m or more. The grass begins growing in late spring and blooms from July to October (Cope, 1982).

Blue panic is a highly productive grass with considerable nutritional value that can produce 150–180 tons of fresh biomass per hectare per year with 15–18% protein content (Bokhari et al., 1987). It has proven to be a valuable cultivated fodder grass (Chaudhary, 1989). In comparison with other forage crops, blue panic is more productive and nutritionally more acceptable (Bokhari et al., 1987), particularly for cattle (Sarwar et al., 2006). *P. antidotale* is used by several wildlife species, such as antelope and California jackrabbits [Tucson Plant Materials Center (http://www.az.nrcs.usda.gov)]. Blue panic has a good economic value for wildlife and livestock, but it can cause nitrate poisoning when grazed where it is richly fertilized (Davidson et al., 1941; McGinty

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and Machen, 1993; Wright and Davidson, 1964). Bluegrass is known to withstand multiple stresses, mainly salinity, drought, fire, etc. Its suitability to highly saline (Bokhari et al., 1987; Cope, 1982), alkaline (Ryan et al., 1975), drought-hit (Bokhari et al., 1987; Chaudhary, 1989; Cope, 1982), and waterlogged (Ashraf, 2004) soils shows its adaptation to a wide range of environmental conditions.

It is now well evident that stress tolerance is a complex multigenic trait (Ashraf and Harris, 2004; Niknam and Mccomb, 2000) involving a multitude of mechanisms, which makes it more difficult to study inheritance of salinity tolerance. It has also been reported that in some species acquired salt tolerance can be passed on to offspring (Niknam and Mccomb, 2000). So potential populations need to be identified and used for growing in highly stressful environments.

Since *P. antidotale* has been found growing on a variety of habitats (Ashraf, 2003), there would be a fair chance of hunting highly salt-tolerant populations from such diverse habitats, in the framework of the present investigations in the surroundings of the Faisalabad, Pakistan, region. Such highly salt-tolerant populations of *P. antidotale* can be selected and used for economic utilization of salt-affected soils. Thus, the main objective of the present study was to assess, up to what extent a high selection pressure has brought about the evolution of salt tolerance in *P. antidotale*. A further objective was to find out whether the accumulation of potential osmoprotectants, such as glycinebetaine and proline, as well as ratios between Na^+, K^+, and Ca^{2+}, are positively related to the degree of salt tolerance of different *P. antidotale* populations collected from different habitats varying in salt content.

Materials and methods

Six populations of *P. antidotale* Retz. were collected in June 2005 from different sites varying in soil salt content (Table 1). Plants of each population were uprooted in four replicates form their parent habitats. Composite soil samples (500 g) were also collected at a depth of 30 cm for the determination of soil electrical conductivity (ECe) and pH. All the plants were established in pots containing normal soil in the Botanical Garden of the Department of Botany, University of Agriculture Faisalabad, and were allowed to grow for 6 months under natural conditions. Ten newly grown tillers of comparable size from each replicate of each population were transplanted equidistant in plastic containers each containing 10 l of half strength Hoagland's nutrient solution (Hoagland and Arnon, 1950) and allowed to establish for 21 days. Theses populations were then exposed to 0 (normal) or 150 mol m^{-3} (saline) NaCl for a period of 42 days. The desired salt level was obtained by an increment of 50 mol m^{-3} NaCl on alternate days. The solution was continuously aerated for 6 h daily during the whole experiment period and renewed regularly after one week. During the course of experiment, the average day and night temperatures were 37 ± 3 and 24 ± 3 °C, respectively, and photoperiod lasted for 11–12 h. Relative humidity of the air ranged from 45.9% to 58.6%.

Growth variables

After 42 days, lengths of the longest culm (from the base to the top leaf excluding panicle) and the longest root were measured. Excised culms and roots were washed with distilled water and their fresh weights recorded. They were then oven dried at 65 °C for 7 days for recording their dry weights.

Water relations

A fully expanded youngest leaf (fourth from the top) was excised from each plant and a pressure bomb apparatus (Chas W. Cook Division, Birmingham, England) was used to measure leaf water potential (Ψ_w). The same leaf was frozen in a freezer for 2 weeks, thawed, and the frozen sap was extracted by crushing the material with a glass rod. The sap was centrifuged (8000*g*) for 4 min and used for osmotic potential (Ψ_s) determination using a vapour pressure osmometer (Wescor 5520, Logan, USA). Leaf pressure potential (Ψ_p) was calculated as the difference between leaf osmotic potential and water potential. Whereas, leaf osmotic adjustment was calculated by the difference between osmotic potentials of treated and control plants.

Photosynthetic variables

Instantaneous measurements of net CO_2 assimilation rate (P_n) and transpiration rate (E) were made on fully expanded youngest leaves (4th leaf from top) using an open system LCA-4 ADC portable infrared gas analyzer (Analytical Development Company, Hoddesdon, England). These measurements were performed at 11:00 a.m. with the following conditions: atmospheric pressure 97.8 kPa, molar flow of air per unit leaf area 408.5 mmol m^{-2} s^{-1}, water vapour pressure inside the chamber ranging from 11.2 to 12.2 mbar, maximum temperature of leaf up to 34.4 °C,

Table 1
Description of the collection sites of the six *Panicum antidotale* populations.

Pop.	Collection site	Coordinates	Soil ECe (dS m^{-1})	Soil pH	Climatic conditions[a]
P1	Salt-affected area of Pakka Anna, Faisalabad	31°19′26.20″N; 72°45′38.49″E	19.23	6.75	Altitude = 213 m; Min. temp. = 2 °C; Max. temp. = 47 °C; Average temp. = 24 °C; Average rainfall = 300 mm
P2	The bank of disposal water channel, Rajawala, University of Agriculture Faisalabad	31°25′30.61″N; 73°03′53.84″E	14.87	6.45	
P3	The barren area of Punjab Wild Life Research Institute (PWRI), Faisalabad	31°28′51.27″N; 73°12′46.78″E	9.31	7.65	
P4	The bank of canal (PWRI), Faisalabad	31°28′26.21″N; 73°12′13.78″E	7.19	6.68	
P5	Botanical Garden Research Area, University of Agriculture, Faisalabad	31°25′43.96″N; 73°04′17.40″E	4.83	6.10	
P6	Forest plantation (*Eucalyptus* spp.) PWRI, Faisalabad	31°28′36.00″N; 73°12′38.51″E	3.39	5.86	

[a] *Source*: Climatological Data Processing Centre, Pakistan Meteorological Department, Karachi, Pakistan; http://www.met.gov.pk/cdpc/home.htm.